

“Data for the Problem of Evolution in Man. IV. Note on the Effect of Fertility depending on Homogamy.” By KARL PEARSON, F.R.S., University College, London. Received March 12,—Read March 29, 1900.

1. In a paper recently contributed to the ‘Proceedings of the Royal Society,’ “Data for the Problem of Evolution in Man. III. On the Magnitude of Certain Coefficients of Correlation in Man,”\* &c., I dealt with the problem of the possible dependence of fertility on homogamy, and I used the following words (p. 29) :—

“When any form of life breaks up into two groups under the influence of natural selection, what is to prevent them intercrossing and so destroying the differentiation at each fresh reproductive stage?”

The answer I suggested was twofold—(i) homogamy, which I can demonstrate to actually exist in the case of man, and (ii) a possible dependence of fertility on homogamy, which would render the cross unions relatively sterile. Either (i) or (ii) would be effective, but (ii) would have the advantage that it does not presuppose assortative mating; we could have a permanent differentiation even with random mating. In writing the above sentence, I had two further points in mind: (*a*) that reproductive selection, while quite capable of producing an evolution, a progressive change in a species, could not by itself differentiate a species into two sub-groups, and (*b*) that no correlation of homogamy with fertility could possibly differentiate a species, however much it might cause the species to progressively change as a whole. My view was that a correlation of homogamy with fertility, together with natural selection, could produce a permanent differentiation of species, but that neither *alone* could be effectual. It was from this standpoint that I concluded my paper with the words :—

“I can conceive no more valuable investigation than a series of experiments or measurements directed to ascertaining whether homogamy is or is not correlated with fertility” (p. 32).

In writing these words I overlooked a very admirable piece of work by Mr. H. M. Vernon, M.A., published in our own ‘Transactions,’ on “The Relations between the Hybrid and Parent Forms of Echinoid Larvæ.”† Had I been acquainted with this memoir, I should certainly have referred to it. In drawing my attention to it, Mr. Vernon has also referred me to two papers by himself in ‘Natural Science,’ on what he terms “Reproductive Divergence.”‡ While welcoming heartily Mr. Vernon’s facts in the paper on “Echinoid Larvæ,” bearing

\* ‘Proc. Roy. Soc.’ vol. 66, p. 28.

† ‘Phil. Trans.’ B, vol. 190, p. 465—529.

‡ Vol. 11, pp. 181—189 and pp. 404—407.

on the correlation of fertility and homogamy, I want at once to express my entire disagreement with his view of reproductive selection, if he holds it, as he appears to do,\* as a source of divergence or differentiation quite independent of natural selection.

The simple fact is, that if fertility be any function of the organs or relative organs of the parents, having a frequency distribution defined by a normal frequency surface, or by any surface approximating to such a chance distribution, then reproductive selection, whether homogamy or any other factor be present, may, under special circumstances, produce a progressive change in a character; it cannot, unless other factors of evolution, such as natural selection, come into play, produce differentiation.

2. I shall assume throughout my proof that the frequency distributions obey the normal law. Now let one offspring only be taken from each pair of parents, and let the organs in the two parents be  $m_1 + x_1$ ,  $m_2 + x_2$ , and in the offspring  $m_3 + x_3$ , where  $m_1$ ,  $m_2$ ,  $m_3$ , are the respective means; let  $\sigma_1$ ,  $\sigma_2$ ,  $\sigma_3$  be the standard deviations of the three organs, and  $r_{12}$ ,  $r_{23}$ ,  $r_{31}$ , the coefficients of correlation, then the frequency  $\delta x_1 \delta x_2 \delta x_3$  of a triplet of parents and offspring with organs lying between  $x_1$  and  $x_1 + \delta x_1$ ,  $x_2 + \delta x_2$ ,  $x_3$  and  $x_3 + \delta x_3$ , respectively, is determined by†

$$z = \frac{N}{(2\pi)^{\frac{3}{2}} \sigma_1 \sigma_2 \sigma_3 \sqrt{\chi}} \text{ expt. } \left[ -\frac{1}{2\chi} \left\{ \frac{x_1^2}{\sigma_1^2} (1 - r_{23}^2) + \frac{x_2^2}{\sigma_2^2} (1 - r_{31}^2) + \frac{x_3^2}{\sigma_3^2} (1 - r_{12}^2) - 2(r_{12} - r_{23}r_{31}) \frac{x_1 x_2}{\sigma_1 \sigma_2} - 2(r_{23} - r_{31}r_{12}) \frac{x_2 x_3}{\sigma_2 \sigma_3} - 2(r_{31} - r_{12}r_{23}) \frac{x_3 x_1}{\sigma_3 \sigma_1} \right\} \right],$$

where  $\chi = 1 - r_{12}^2 - r_{23}^2 - r_{31}^2 + 2r_{12}r_{23}r_{31}$ ,

and  $N$  = total number of pairs of parents.

If, instead of the single offspring, we take  $n$ , we have only to replace  $N$  in the above results by  $nN$ .

Now reproductive selection supposes the fertility of a given pair not to be independent of the measure of their organs, in this case of  $m_1 + x_1$  and  $m_2 + x_2$ .

If we suppose  $n$  to represent the total fertility of a given pair, we

\* "This divergence of species takes place quite independently of natural selection, but this principle can always be exerting its action at the same time, whereby the new or modified characteristics produced can, if useful to the species, be accumulated and rendered better adapted to the environmental conditions." 'Natural Science,' vol. 11, p. 186.

† 'Phil. Trans.' A, vol. 187, p. 287.

shall, on the hypothesis of the normal law holding for frequency of offspring, have

$$n = n_0 e^{-\frac{1}{2} \frac{y^2}{s^2}},$$

where  $y$  is the deviation of some character based upon both parental organs from the value which gives the maximum fertility, and  $s$  is its standard deviation.

Thus,  $c$  and  $a$  denoting constants,

$$\begin{aligned} y &= f(m_1 + x_1, m_2 + x_2) \\ &= c_0 + c_1 x_1 + c_2 x_2 + \text{higher terms in } x_1 \text{ and } x_2; \end{aligned}$$

hence 
$$y^2 = a_0 + a_1 x_1 + a_2 x_2 + a_3 x_1^2 + 2a_4 x_1 x_2 + a_5 x_2^2,$$

if we neglect higher powers of  $x_1$  and  $x_2$ . This will, as a rule, be justified if  $x_1$  and  $x_2$  are small as compared with  $m_1$  and  $m_2$ .

We conclude that :

$$n = n_0 \text{ expt. } \left[ -\frac{1}{2s^2} (a_0 + a_1 x_1 + a_2 x_2 + a_3 x_1^2 + 2a_4 x_1 x_2 + a_5 x_2^2) \right].$$

If we multiply this by  $z$ , we have the distribution of parents and offspring, allowing for a varying fertility. Let this be  $z'$ , then it will be at once obvious that

$$z' = \text{const.} \times \text{expt. } [- (\text{quadratic expression in } x_1, x_2)].$$

Hence if we integrate for  $x_1$  and  $x_2$ , so as to get the distribution of the offspring, we find it again given by a normal curve, *i.e.*, a curve symmetrical about its mode. *Thus a progressive change, but no differentiation, can be produced by reproductive selection.*

This is the proof, of which I merely stated the result in my "Note on Reproductive Selection" of 1895.\* The same view was again expressed in my memoir on "Genetic (Reproductive) Selection" of 1898.† While reproductive selection is invaluable as an aid to natural selection, alone it can only progressively modify not differentiate a race. For such differentiation we should have to suppose some much more elaborate relation between fertility and the complex of parental organs than is indicated by a normal chance distribution.

3. In order to show what would occur supposing fertility reached a maximum with homogamous unions, I do not simply take  $y$  to be the difference of the parental organs, for it is quite conceivable that the organs may be sexual characters, and differ not only in magnitude but even qualitatively. I accordingly suppose the fertility to be a maximum

\* 'Roy. Soc. Proc.,' vol. 59, p. 303.

† 'Phil. Trans.,' A, vol. 192, p. 314.

when the two organs bear a certain ratio to each other. For example, we hardly mean by a homogamous union in man and woman with regard to stature, a case of husband and wife of equal height, but rather a case of their being *relatively* of equal height, or, say, the ratio of their statures = 1.08.\*

For this reason I put

$$y = p_1(m_1 + x_1) - p_2(m_2 + x_2),$$

and asked Mr. L. N. G. Filon, M.A., to work out for me the constants of the correlation surface, whose ordinate is  $z' = z \times n$ . He has kindly provided me with the following results, the analysis being straightforward but lengthy.

Let  $m_1 + h_1$ ,  $m_2 + h_2$  be the mean values of the organs in the parents, each parent being repeated for each of his or her offspring.  $m_3 + h_3$  = mean value of offspring's organ, or  $h_3$  be the progression in the character due to the influence of homogamy.

$\Sigma_1$ ,  $\Sigma_2$ , the standard deviations of the parents' organs, these being, as in the case of  $h_1$  and  $h_2$ , weighted with their fertility.

$\Sigma_3$  = standard deviation in offspring's organ, or  $\Sigma_3 - \sigma_3$  is the change in variability due to the homogamous influence.

$\rho_{31}$ ,  $\rho_{32}$  = the correlations between parent and offspring when we take *all*, and not a single offspring from each union.

$\rho_{12}$  the coefficient of assortative mating when we take each pair as many times as there are offspring of the union.

We have:

$$\frac{h_1}{\sigma_1} = \frac{h_2}{\sigma_2} = -\frac{(p_1\sigma_1 - p_2\sigma_2)(p_1m_1 - p_2m_2)}{s^2 + (p_1\sigma_1 - p_2\sigma_2)^2} \dots\dots\dots (i).$$

$$\frac{h_3}{\sigma_3} = -\frac{r_{31} + r_{32}}{1 + r_{12}} \frac{(p_1\sigma_1 - p_2\sigma_2)(p_1m_1 - p_2m_2)}{s^2 + (p_1\sigma_1 - p_2\sigma_2)^2} \dots\dots\dots (ii).$$

This last result may be written

$$\frac{h_3}{\sigma_3} = \frac{r_{31} - r_{12}r_{32}}{1 - r_{12}^2} \frac{h_1}{\sigma_1} + \frac{r_{32} - r_{12}r_{31}}{1 - r_{12}^2} \frac{h_2}{\sigma_2} \dots\dots\dots (iii).$$

$$\Sigma_1^2 = \sigma_1^2 \left( 1 - \frac{(p_1\sigma_1 - r_{12}p_2\sigma_2)^2}{s^2 + p_1^2\sigma_1^2 + p_2^2\sigma_2^2 - 2r_{12}p_1p_2\sigma_1\sigma_2} \right) \dots\dots\dots (iv).$$

$$\Sigma_2^2 = \sigma_2^2 \left( 1 - \frac{(r_{12}p_1\sigma_1 - p_2\sigma_2)^2}{s^2 + p_1^2\sigma_1^2 + p_2^2\sigma_2^2 - 2r_{12}p_1p_2\sigma_1\sigma_2} \right) \dots\dots\dots (v).$$

$$\Sigma_3^2 = \sigma_3^2 \left( 1 - \frac{(r_{13}p_1\sigma_1 - r_{23}p_2\sigma_2)^2}{s^2 + p_1^2\sigma_1^2 + p_2^2\sigma_2^2 - 2r_{12}p_1p_2\sigma_1\sigma_2} \right) \dots\dots\dots (vi).$$

\* This is how I have looked at the matter in "Data for the Problem of Evolution in Man. III," 'Roy. Soc. Proc.,' vol. 66, p. 31.

$$\rho_{12} = \frac{r_{12} + \frac{p_1 p_2 \sigma_1 \sigma_2}{s^2} (1 - r_{12}^2)}{\sqrt{\left\{ 1 + \frac{p_1^2 \sigma_1^2}{s^2} (1 - r_{12}^2) \right\} \left\{ 1 + \frac{p_2^2 \sigma_2^2}{s^2} (1 - r_{12}^2) \right\}}} \dots\dots \text{(vii).}$$

$$\begin{aligned} \rho_{31} &= \frac{r_{31} + \frac{p_1 p_2 \sigma_1 \sigma_2}{s^2} (r_{32} - r_{12} r_{31}) + \frac{p_2^2 \sigma_2^2}{s^2} (r_{31} - r_{12} r_{32})}{\sqrt{1 + \left\{ \frac{p_1^2 \sigma_1^2}{s^2} (1 - r_{31}^2) + \frac{p_2^2 \sigma_2^2}{s^2} (1 - r_{32}^2) - \frac{2 p_1 p_2 \sigma_1 \sigma_2}{s^2} (r_{12} - r_{31} r_{32}) \right\} \times}} \\ &\quad \sqrt{\left\{ 1 + \frac{p_2^2 \sigma_2^2}{s^2} (1 - r_{12}^2) \right\}} \dots\dots\dots \text{(viii).} \end{aligned}$$

$$\begin{aligned} \rho_{32} &= \frac{r_{32} + \frac{p_1 p_2 \sigma_1 \sigma_2}{s^2} (r_{31} - r_{12} r_{32}) + \frac{p_1^2 \sigma_1^2}{s^2} (r_{32} - r_{12} r_{31})}{\sqrt{\left\{ 1 + \frac{p_1^2 \sigma_1^2}{s^2} (1 - r_{31}^2) + \frac{p_2^2 \sigma_2^2}{s^2} (1 - r_{32}^2) - \frac{2 p_1 p_2 \sigma_1 \sigma_2}{s^2} (r_{12} - r_{31} r_{32}) \right\} \times}} \\ &\quad \sqrt{\left\{ 1 + \frac{p_1^2 \sigma_1^2}{s^2} (1 - r_{12}^2) \right\}} \dots\dots\dots \text{(ix).} \end{aligned}$$

Results (i) to (ix) contain the whole theory of the influence on evolution of a relation between homogamy and fertility.

4. *General Conclusions.*—(a) There is in general a progressive change in the species as a whole, but no divergence or differentiation.

(b) The change in the second generation (as given by (iii)) is precisely what we might have anticipated from my theory of biparental inheritance,\* assuming that the offspring are those of parents differing from the general population by an amount of the character which is the excess marking parents weighted by their fertility from the general parental population.

(c) The offspring will be less variable than they would be without a correlation between homogamy and fertility, *i.e.*, from (vi)  $\Sigma_3$  is always less than  $\sigma_3$ .

\* 'Roy. Soc. Proc.' vol. 58, p. 240, or 'Phil. Trans.' vol. 187, p. 287. Another interesting relation of this kind is the following one:

$$\sigma_3 \sqrt{\frac{1 - r_{12}^2 - r_{23}^2 - r_{31}^2 + 2r_{12}r_{23}r_{31}}{1 - r_{12}^2}} = \Sigma_3 \sqrt{\frac{1 - \rho_{12}^2 - \rho_{23}^2 - \rho_{31}^2 + 2\rho_{12}\rho_{23}\rho_{31}}{1 - \rho_{12}^2}};$$

or the variability of an array of offspring from selected parents is unaltered by the relation between homogamy and fertility—a result which might be *a priori* expected.

(d) The coefficient of assortative mating  $\rho_{12}$  for parents weighted with their fertility differs sensibly from that of unweighted parents  $r_{12}$ . Generally the effect of a relation between homogamy and fertility is to increase the apparent coefficient of assortative mating.

(e) The coefficients of parental heredity are also modified when we take all and not a single representative of the offspring.

5. *Special Conclusions.*—These depend on how we define *homogamy*. When would the male and female be “alike”? Mr. Francis Galton, in the case of stature in man, reduces the female to the male equivalent by altering her stature in the ratio of mean male to mean female stature. In my paper on the Law of Ancestral Heredity\* I give reasons for using as a factor of reduction the ratio of the male standard deviation to the female standard deviation. Mr. Galton’s method and mine agree fairly closely in the case of man, for the coefficients of variation† of man and woman (*i.e.*,  $100\sigma_1/m_1$  and  $100\sigma_2/m_2$  in our present notation) are nearly equal for a considerable variety of organs. In either case we should understand by a homogamous union one in which the female organ reduced to the male equivalent was exactly equal to the male organ. Accordingly the ratio of  $p_1$  to  $p_2$  would be that of  $m_2$  to  $m_1$ , or of  $\sigma_2$  to  $\sigma_1$  according to the hypothesis adopted. In the case of man, if either hypothesis be used, the other would be nearly satisfied. Hence, with a reasonable hypothesis as to what we mean by homogamy, it follows that—

(a) No progressive change in the mean would arise in a species owing to a relation between homogamy and fertility ( $h_3 = 0$ , since either  $p_1/p_2 = m_2/m_1$  or  $\sigma_2/\sigma_1$ ).

(b) With equipotency of hereditary influence in the parents, the race would not on my hypothesis alter its variability, and on Mr. Galton’s hypothesis only by an extremely small quantity of the fourth order (if  $r_{13} = r_{23}$ , then by (vi)  $\Sigma_3$  differs from  $\sigma_3$  by a term of the order  $r_{13}^2(p_1\sigma_1 - p_2\sigma_2)^2$ ).

(c) The coefficient of assortative mating will be increased. For if  $p_1\sigma_1/s = p_2\sigma_2/s = \tau$ , then

$$\rho_{12} = \frac{r_{12} + \tau^2(1 - r_{12}^2)}{1 + \tau^2(1 - r_{12}^2)},$$

which is greater than  $r_{12}$ . If  $r_{12} = 0$ , then  $\rho_{12} = \tau^2/(1 + \tau^2)$ , or a relation between homogamy and fertility would produce an apparent correlation between husband and wife, if we weighted them with their fertility, although they exercised no selective mating. This increase of  $\rho_{12}$  is in complete agreement with the result obtained for the coefficient

\* ‘Roy. Soc. Proc.’ vol. 62, p. 390.

† ‘Phil. Trans.’ A, vol. 187, p. 276.

of assortative mating in the paper\* “Data for the Problem of Evolution in Man. III.”†

(d) The parental coefficient of heredity will generally be increased by taking all instead of a single one of the offspring.

For example, putting  $r_{12} = 0$ ,  $p_1\sigma_1/s = p_2\sigma_2/s = \tau$  as before, we find for equipotency—

$$\rho_{12} = \tau^2/(1 + \tau^2), \quad \rho_{31} = \rho_{32} = r_{31} \sqrt{(1 + 2\tau^2)/(1 + \tau^2)}.$$

Thus

$$\rho_{31} = r_{31} \sqrt{1 + \rho_{12}},$$

showing how the spurious coefficient of assortative mating modifies the coefficient of inheritance.

6. Thus I think it will be clear that *Reproductive Divergence* has not an effective existence. More generally *Reproductive Selection*, unless we suppose *ab initio* a fertility distribution with two modes (which is not given by homogamy, and wants, in any case, a special explanation), will not produce differentiation. It can produce, as I have often stated, progressive change. So far as I can yet see, differentiation must involve natural selection, and one can only appeal to reproductive selection as a means, but I think an effective means, of maintaining a differentiation already brought about by Darwin's fundamental factor in evolution.

Mr. Vernon, in his first paper, states that given a relationship between homogamy and fertility, then reproductive divergence “is capable of mathematical demonstration. This we will now proceed to afford” (p. 182).

In his second paper, he gives what he terms “the mathematical basis of the theory more fully” (p. 404). I venture to think that the whole of his treatment is fallacious. In the first paper he neglects the Law of Regression, and he thinks this justifiable, but it is not so. In

\* ‘Roy. Soc. Proc.’ vol. 66, p. 30.

† Assuming equipotent hereditary influence of father and mother for stature, we have from the above paper—

$$\rho = 0.1783, \quad r_{12} = 0.0931, \quad \text{and} \\ \tau^2 = (\rho_{12} - r_{12}) / \{ (1 - \rho_{12}) (1 - r_{12}^2) \} = 11.9626.$$

Hence  $p_1\sigma_1/s = p_2\sigma_2/s = \tau = 3.4587$ . Thus from the equation for  $y$  we find

$$\frac{y}{s} = 3.4587 \left( \frac{m_1 + x_1}{\sigma_1} - \frac{m_2 + x_2}{\sigma_2} \right).$$

If  $X_1 = m_1 + x_1$  = stature of father,  $X_2 = m_2 + x_2$  = stature of mother, we have for the relation between fertility and homogamy

$$n = n_0 e^{-\frac{11.9626}{2} \left( \frac{X_1}{\sigma_1} - \frac{X_2}{\sigma_2} \right)^2}.$$

This will suffice to indicate how such relations can be numerically investigated.

the second paper he takes an arithmetical example based on 205 families. His results, if correct, would only show a flattening of the frequency-curve, an increased variability, and not a divergence or differentiation. But I have shown that the tendency is really to a decreased variability, and on examination it will be found that the differences on which Mr. Vernon bases his conclusions are all of the order of the probable errors of his results! Apart from this, however, the whole of his argument on pp. 405-6 seems to me invalid; we cannot proceed by a vague threefold classification such as he adopts; and he nowhere introduces, so far as I can see, the difference in height of the parents which must be the essential feature of the whole argument.

That Mr. Vernon has shown a relationship between homogamy and fertility in his 'Phil. Trans.' memoir is of high value, but I hold that such cannot help us in the *slightest* degree to dispense with the fundamental factor of Darwinian evolution, namely, natural selection.\*

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April 5, 1900.

The LORD LISTER, F.R.C.S., D.C.L., President, in the Chair.

A List of the Presents received was laid on the table, and thanks ordered for them.

In pursuance of notice sent to the Fellows, an election was held to fill the vacancy upon the Council caused by the decease of Mr. G. J. Symons.

The statutes relating to the election of the Council, and the statute relating to the election of a Member of Council upon the occurrence of a vacancy, were read, and Professor Carey Foster and Sir E. Ommanney having been, with the consent of the Society, nominated scrutators, the votes of the Fellows present were taken and Mr. W. H. M. Christie, Astronomer Royal, was declared duly elected.

The following Papers were read :—

I. "On the Weight of Hydrogen desiccated by Liquid Air." By LORD RAYLEIGH, F.R.S.

\* Since the above paper was sent to the Royal Society—

(a) The relationship of eye-colour to fertility in both man and woman has been investigated for several thousand cases; while there appears to be some correlation between eye-colour and fertility, homogamous unions do not appear to be the more fertile. The numbers will be eventually published;

(b) Mr. Vernon has sent me a letter stating that, on further investigation, he has modified his views on *Reproductive Divergence*.